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Revision of the Bee Genus *Agapostemon* (Hymenoptera: Halictidae)^{1,2}

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ABSTRACT

In this study 43 species of *Agapostemon* are recognized from the Americas. Of these, the following 19 species are new: *A. aenigma*, *A. alayoi*, *A. ascius*, *A. boliviensis*, *A. columbi*, *A. cubensis*, *A. cyaneus*, *A. erebus*, *A. hispaniolicus*, *A. inca*, *A. insularis*, *A. intermedius*, *A. jamaicensis*, *A. lanosus*, *A. mexicanus*, *A. mourei*, *A. ochromops*, *A. peninsularis*, *A. sapphirinus*. Forty-six names are listed as synonyms, 26 for the first time. Twenty-two species previously placed in *Agapostemon* but now placed in other genera are listed.

Separate keys are provided for species from America north of Mexico, Meso-America, The West Indies and South America. All species are described and most are illustrated. The geographic distribution and variation of the species and species groups are discussed, with particular regard to speciation of North American groups.

INTRODUCTION

The genus *Agapostemon* occurs only in the Western Hemisphere where it ranges from southern Canada to Paraguay. It is the only member of a group of allied genera to be found north of Mexico—South America being the center of abundance of most of its relatives.

Agapostemon is polythetic and cannot be differentiated from related genera on the basis of any one character or group of characters. Nevertheless, most species are characterized by their metallic green or blue head and mesosoma and their contrasting black or black and yellow metasoma.

Until recently, the biology of this genus was poorly known. However, in 1969 Eickwort and Eickwort described in detail the nesting and foraging behavior of *A. nasutus* in Central America. In the same year I reported on the biology of the North American *A. radiatus*, *A. splendens* and *A. texanus* and summarized available information on other species. These biological investigations have complemented the present classification.

The primary objective of this revision is to describe and classify the species of *Agapostemon* and to elucidate their evolutionary history. It is possible to recognize species groups and in some cases provide reasonable

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explanations of their origins, but the number of species with no apparent affinities proscribes extensive speculation on the phylogeny of the genus.

A second objective of this work is to facilitate identification of species of *Agapostemon*. To this end keys, descriptions and illustrations have been prepared in as simple and uniform a style as possible. Species descriptions are in alphabetical sequence, because I believe a phenetic or "phylogenetic" sequence presumes too much knowledge on the part of the readers. The keys are regional and artificial for the sake of brevity and clarity respectively.

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HISTORICAL REVIEW

The taxon *Agapostemon* was first proposed in 1844 by F. E. Guérin-Méneville as a subgenus of *Andrena* in the following statements:

Nous connaissons plusieurs espèces à cuisses ainsi renflées. Ce sont des mâles. Peut-être jugera-t-on à propos de les réunir en un sous-genre, que nous proposerions de nommer *Agapostemon*. Il serait aux *Andrenes* ce qu'est le genre *Nomia* parmi les *Halictes*.

The only included species was *Andrena (Agapostemon) femoralis* Guérin 1844. Dalla Torre (1896) correctly recognized this species to be a junior synonym of *Apis viridula* Fabricius 1793. Therefore the correct name for the type species of the genus *Agapostemon* is now *Agapostemon viridulus* (Fabricius). *Agapostemon* was first described and accorded generic rank in 1853 by Frederick Smith, who listed seven species, four of them new. In 1896 Dalla Torre catalogued 16 species and placed four species in synonymy. He also gave the Latin translation of Guérin's transliterated Greek compound, *Agapostemon*, as "ἀγαπω αμο, στημων *stemen*." In English the translation is "lover of stamens."

In 1897 Robertson redescribed the species known from the United States and listed their synonyms. The first key, published by Titus in 1901, included only the species known to occur in Colorado, and in November of the same year Crawford revised the North American species of *Agapostemon*. In this revision Crawford re-described the genus, described seven new species, and included a key to the 15 species then known from North America. In 1902 Robertson published keys to the genera and species of the North American Halictinae in which he commented on the relationships of the genera. Although he cited very few characters, the keys and generic concepts were remarkably good.

In 1903 Vachal reduced *Agapostemon* to subgeneric rank in *Halictus*. He included 28 species (nine of them new) in the subgenus *Agapostemon* and proposed the new subgenus *Paragapostemon* for 25 additional species

with hairy eyes and without a complete propodeal carina. Although his keys were good, Vachal's conservative generic concepts were not widely accepted, and Cockerell (1905) accorded generic rank to both *Agapostemon* and *Paragapostemon*. Vachal did not cite a type species for *Paragapostemon*, but Cockerell (1905, in footnote) designated *Halictus (Paragapostemon) podager* Vachal as the type species.

Schrottky (1909a) erected the genus *Pseudagapostemon* (type species *Agapostemon arenarius* Schrottky), thereby removing most of the species from *Paragapostemon* as well as additional species from *Agapostemon*. Schrottky published another paper (1909b) in which he reduced seven species of South American *Agapostemon* to synonymy and transferred four more from *Agapostemon* to *Pseudagapostemon*. In 1918(a) Cockerell reduced *Pseudagapostemon* to subgeneric rank in *Agapostemon*, but never referred to it as such thereafter.

In 1936 Sandhouse revised the species of *Agapostemon* occurring in the United States. Although she examined about 4,000 specimens, her work does not make sufficient allowance for intraspecific variation, none of the species are described, the only figures (of genitalia) are inadequate, and finally, she did not recognize five of the species now known from the United States; *A. femoratus*, *A. tyleri*, *A. nasutus*, *A. peninsularis* and *A. leunculus*. Despite these shortcomings, Sandhouse's revision has remained the best available reference on the genus for more than thirty years. More recent systematic treatments of *Agapostemon* are the contribution by Michener (1951) to the catalog of North American Hymenoptera; and the key, descriptions and figures for the species in the eastern United States (Mitchell, 1960).

EXCLUDED SPECIES

The following is a list of species which, although described in or subsequently transferred to *Agapostemon*, are no longer considered to belong to this genus. When possible the genus to which they belong has been indicated. Some of the species are synonyms but listing of synonymies must be postponed until *Paragapostemon* and *Pseudagapostemon* can be revised.

In 1918(a) Cockerell reduced *Pseudagapostemon* to a subgenus of *Agapostemon* but this classification has never won acceptance. The only species mentioned by Cockerell [*Agapostemon (Pseudagapostemon) xanthorhinus* Cockerell, *Halictus citricornis* Vachal, *Pseudagapostemon paulista* Schrottky, and *Pseudagapostemon nasua* Schrottky] have been omitted from the following list.

Augochloropsis

Agapostemon caeruleus Ashmead 1890 was placed in *Augochloropsis* by Titus (1901).

Paragapostemon

Nomia caelestina Westwood 1875, placed in *Agapostemon* by Cockerell (1910a), was placed in *Paragapostemon* by Moure (1964).

Agapostemon bruneri Crawford 1901 was placed in *Paragapostemon* by Moure (1964).

Halictus (Agapostemon) sicheli Vachal 1901 was placed in *Paragapostemon* by Moure (1964).

Nomia tacita Cameron 1902, placed in *Agapostemon* by Cockerell (1910a), was placed in *Paragapostemon* by Moure (1964).

Nomia cillaba Cameron 1902, placed in *Agapostemon* by Cockerell (1910a), was placed in *Paragapostemon* by Moure (1964).

Ruizantheda

Halictus emarginatus Spinola 1851, placed in *Agapostemon* by Cockerell (1905), is a synonym of the type species (*Halictus proximus* Spinola 1851) of *Ruizantheda* Moure 1964.

Halictus mutabilis Spinola 1851, placed in *Agapostemon* by Schrottky (1903), became the type species of *Ruizantheda (Ruizanthedella)* Moure 1964.

Halictus placidus Smith 1879 was placed in *Agapostemon* by Cockerell (1905), but Moure (*in litt.*) places it in *Ruizantheda*.

Pseudagapostemon

Agapostemon arenarius Schrottky 1902(b) became the type species of *Pseudagapostemon* Schrottky 1909(a).

Agapostemon aeneus Schrottky 1902(a) was placed in *Pseudagapostemon* by Schrottky (1909b).

Agapostemon arechavaletae Schrottky 1908 was placed in *Pseudagapostemon* by Schrottky (1909b).

Agapostemon bonaërensis Schrottky 1908 was placed in *Pseudagapostemon* by Schrottky (1909b).

Halictus (Agapostemon) pissisi Vachal 1903 was placed in *Pseudagapostemon* by Vachal (1904).

Halictus (Agapostemon) divaricatus Vachal 1903 was placed in *Pseudagapostemon* by Vachal (1904).

Agapostemon olivaceo-splendens Strand 1910 was placed in *Pseudagapostemon* by Moure (1947).

Agapostemon zosteronedys Moure 1940 belongs in *Pseudagapostemon divaricatus* (Vachal) as indicated by Moure (footnote in Michener and Lange, 1958).

Species Incertae Sedis

Halictus bruchianus Schrottky 1908 was placed in *Agapostemon* by Schrottky (1913). Moure (*in litt.*) has not seen the type but believes it should be placed in *Corynura* or *Ruizantheda* (probably the latter).

GENERIC DIAGNOSIS

No one character or set of characters was found to be both necessary and sufficient to distinguish all species of *Agapostemon* from all species in other halictine genera. However, the genus may be recognized by a syndrome of characters. This set of characters is common to most species of *Agapostemon* but not all of its characters are present in all of the species.

The character which is unique to *Agapostemon* and which best separates this genus from other halictine genera is the carina which in most species entirely surrounds the posterior surface of the propodeum of both sexes. Also unique among halictines is the striking contrast between the non-metallic coloration of the metasoma and the metallic coloration of the head and mesosoma of most female and nearly all male *Agapostemon*.

Female *Agapostemon* may be distinguished from females of most other halictine genera by the three or four (sometimes as many as seven) large spatulate teeth on the posterior hind tibial spur and by the parallel contiguous carinae extending postero-dorsally from the antero-ventral margin of the gena. Male *Agapostemon* may be distinguished from males of the augochlorine genera and the genera in the *Halictus-Lasioglossum* group by the fusion of the first two tarsomeres of the hind tarsus. Unlike those of almost all other halictine genera, the hind femora and, to a lesser extent, the hind tibiae of many male *Agapostemon* are conspicuously swollen. The only other genera with similarly modified legs have conspicuously hairy eyes in contrast to the glabrous or nearly glabrous eyes of *Agapostemon*.

INFRAGENERIC STRUCTURE

While it seems premature to speculate at length on the phylogeny of the species of *Agapostemon*, certain discrete groups of species can be recognized on the basis of such features as genitalia, pronotum, legs, metasomal sterna and color pattern. These species groups might have been recognized as subgenera, but to be consistent I would have been forced to recognize an unacceptable number of small or monotypic subgenera. Subspecies are not recognized because there is little biological or utilitarian justification for such in this genus. Of course, intra-specific variation is described wherever encountered.

In the following list the name of the first member (chosen arbitrarily) of each species group has not been indented and will serve to identify the group in subsequent discussion (e.g., the species in the *splendens* group are *A. splendens*, *A. texanus* and *A. angelicus*).

kohliellus
centratus
poeyi
insularis
jamaicensis
viequesensis
columbi
ochromops
sapphirinus
cyaneus
aenigma
viridulus
obscuratus
hispaniolicus
cubensis
alayoi
swainsonae

WEST
INDIAN

splendens
texanus
angelicus
*radiatus**
cockerelli
*femoratus**
*virescens**
tyleri
*coloradinus**
melliventris
peninsularis
mexicanus

MESO-AMERICAN
(except those
with asterisk)

rhopalocera
erebus

ascius
leunculus
nasutus
atrocaeruleus
*semimelleus**
*chapadensis**
intermedius

SOUTH
AMERICAN
(except *atrocaeruleus*)

heterurus
inca
mourei
boliviensis
lanosus

ZOOGEOGRAPHY

Although more than 50,000 specimens were examined in the course of this study, I was hampered by inadequate collections from the West Indies as well as Central and South America. While it seems unlikely that any new North American species will be discovered, it is likely that new species remain to be found in the West Indies, Central America and the Andean region of South America.

It is difficult to comprehend what factors influence the distribution of species of *Agapostemon*. Only in the correlation between the distribution of *A. splendens* and that of moist sandy soils in the eastern United States and eastern Mexico is there evidence of a causal relation between the presence of an ecological parameter and the presence of the bees (Roberts, 1969).

Some species, such as *A. coloradinus*, are relatively restricted in range while others are widespread, *A. texanus* occurring from Canada to Costa Rica and Boston to San Francisco. In the United States alone, *A. texanus* occurs in 70 of 116 plant communities (Appendix A). *A. angelicus* occurs from below sea level in Death Valley, California to 12,000 ft. (3,658 m) on Mt. Evans in Colorado (timberline 11,700 ft.). In view of the apparent ecological plasticity among most species, it is not surprising that their distributions broadly overlap.

North American Species. There are four North American species groups. Each of these groups is composed of two very similar species and a third species which, although obviously closely related, stands somewhat apart phenetically. In each group but one, the two most similar species are found west of the 95th meridian and the third species is found north and east of the others. There is some sympatry within each species group, but the center of distribution is different for each species within a group (Fig. 228).

The simplest explanation for the occurrence of these similar geographic and cladistic patterns in each of the North American species groups is to assume: (1) North America was originally occupied by four species; (2) each species was bisected into southeastern and southwestern populations at the time of Pleistocene glaciation; and (3) the southwestern populations were more recently subdivided (possibly on the Pacific and Gulf coasts of Mexico) when forced to migrate farther south by still further cooling. Presumably this pattern of evolution is not evident among the Meso-American and West Indian species groups because they were too far south to have been significantly displaced by the climatic changes accompanying Pleistocene glaciation.

West Indian Species. The West Indian species are interesting in that they are not found on the mainland (with the doubtful exception of *A.*

aenigma) and are not closely related to the mainland species. This is somewhat surprising in view of their relative proximity to the Florida and Yucatan peninsulas. Also surprising is their absence in the lesser Antilles; yet their occurrence throughout the Bahama Islands and Greater Antilles constitutes prima-facie evidence of high vagility.

Although it is extremely improbable that the bees fly of their own accord between islands, it does seem likely that they are occasionally swept up by hurricanes and deposited on other islands many miles distant. Members of the *poeyi* and *viridulus* groups are widespread (cf. map, Fig. 1). As there is very little discernible correlation of geographic factors with the phenotype among members of each of these phenetically homogeneous species groups, I am inclined to believe that, relative to their rates of evolution, their rates of dispersal have been rapid.

In studying the *poeyi* group I vacillated between considering all of the island populations as conspecific and considering each population as a separate species. *A. poeyi* and *A. viequesensis*, occurring in Cuba and Puerto Rico respectively, have long been considered as distinct species which could easily be differentiated morphologically. However, as morphologically intermediate forms exist on the Bahama Islands, it is tempting to classify the entire group as a single highly variable species. However, phenetically typical populations of *A. poeyi* and *A. viequesensis* are sympatric on New Providence Island, and there is no evidence of hybridization. The phenetic homogeneity within each of the phenetically different populations of this complex on other islands leads me to believe that gene flow between these allopatric populations is also inconsequential. Thus it seems that in the *poeyi* group the rate of speciation, or creation of clades, is high relative to the rate of evolution, or shift in gene frequency. Although not as large and widespread, the *viridulus* group similarly appears to be speciating relatively rapidly. My decision to regard the *A. poeyi* group as an *Artenkreis* rather than a *Rassenkreis* is based on scanty evidence. However, the decision is a taxonomic necessity which in no way effects the biological attributes of the organisms in question.

The species *A. kohliellus* and *A. centratus* do not seem closely related to any other species of *Agapostemon*. Rare species, they may be restricted to a particular ecological factor found only on the island of Hispaniola. Such a severe ecological limitation could explain their absence on the other islands.

Meso-American Species. The distributions and relationships of the species occurring in this region are difficult to interpret. Some of the species such as *A. mexicanus* or *A. tyleri* clearly belong to North American groups although *A. mexicanus* is found in northwestern Mexico and *A. tyleri* ranges southward on the central plateau to the vicinity of Mexico City.

A. rhopalocera is a rare species known only from males, not obviously

related to other species and restricted to the vicinity of Mount Orizaba in Vera Cruz. *A. erebus* is known from a single female collected in El Salvador, but is obviously closely related to *A. leunculus* which ranges from the southern tip of Texas to eastern Ecuador, and also to a third species, *A. ascius*, known from two females collected in Colombia.

Males of *A. nasutus* are unlike those of any other species inasmuch as their genitalia and clypeal region are both highly modified. They also differ from males of other species in less striking features such as the lateral tufts of pubescence on the 6th metasomal sternum. Despite these obvious peculiarities of males, females of *A. nasutus* are somewhat similar to those of the *erebus* group (differing principally in the shape of the pronotum). The commonest species throughout most of its range, *A. nasutus* is found from the southern tip of Texas to northern South America, as far east as Trinidad, and west of the Andes as far south as Ica, Perú.

A. atrocaeruleus has been found only in Costa Rica but is closely related to a pair of species found primarily south of the Amazon Basin but reaching as far north as Ecuador. *A. intermedius* is found from Costa Rica to Tingo Maria, Perú and obviously links the *atrocaeruleus* group with the Andean *heterurus* group.

In summary, most of the Meso-American species of *Agapostemon* belong in North or South American species groups. Only the very widespread and abundant *A. nasutus* and the very restricted and rare *A. rhopalocera* have no apparent affinities with either North or South American species, or each other.

South American Species. Some of the species occurring in South America such as *A. nasutus*, *A. intermedius* and *A. ascius* are restricted to the northwestern margin of the continent. Apparently these species, which are recently evolved or recently arrived via Central America (e.g., *A. nasutus*), have found further access to the continent blocked by the Andes to the east, the Atacama Desert to the south, and the forests of the Orinoco Basin to the north.

Agapostemon chapadensis and *A. semimelleus* are the only species widely distributed in South America. Both are found in the *campos*, or subtropical grasslands, of southern Brasil, Paraguay and northern Argentina. In addition isolated populations of *A. semimelleus* have been collected from the headwaters of the Marañón, Huallaga and Cauca rivers. Presumably, these species were able to ascend the valleys at some time in the past when the South American grasslands were more extensive than today. Surprisingly, *A. semimelleus* has been collected at the head of the Cauca Valley in Colombia. I cannot explain this occurrence as the Cauca River drains into the Caribbean Sea. Specimens of *A. semimelleus* have been collected from localities as near as the headwaters of the Putumayo River, but the Cauca and Putumayo

rivers are separated by at least 200 kilometers of mountains (Cordillera Central) rising as high as 5755 m. The closest relative of *A. semimelleus* and *A. chapadensis* is *A. atrocaeruleus* which has been collected only on the central plateau of Costa Rica, nearly 1000 km from the headwaters of the Cauca River.

The most aberrant species group in *Agapostemon* includes *A. heterurus*, *A. inca*, *A. boliviensis*, *A. lanosus* and *A. mourei*. These species are very closely related and are restricted to the eastern margins of the central Andes. As many of the valleys in this region are both ecologically isolated and poorly collected, it seems reasonable to predict that more species in this group will be discovered.

A. intermedius is morphologically intermediate between the *A. heterurus* group and the *A. atrocaeruleus* group. *A. intermedius* ranges from central Costa Rica, where it is sympatric with *A. atrocaeruleus*, to northwestern South America. It has also been collected from Tingo Maria at the head of the Huallaga Valley where it is sympatric with *A. lanosus*. Possibly *A. intermedius* is part of an *Artenkreis* running from Costa Rica down to the grasslands of Brasil (the *A. atrocaeruleus* group) and down to the eastern margins of the Andes (the *A. heterurus* group).

METHODS

TERMINOLOGY. The terminology is essentially that utilized by Michener (1944, 1965). However, the following terms have been proposed since no appropriate ones existed for these features.

The *propodeal shield* is the flat or slightly concave area on the posterior vertical surface of the propodeum usually delimited by a conspicuous *propodeal carina* (Fig. 25). Male genitalia often bear an *apical stylus*, *medial plate* and *basal stylus* on the mesal surface of the gonostylus (Fig. 180). Although often reduced and covered by long bristles, a *ventral lobe* (Fig. 223) is always present on the ventral surface of the gonocoxite.

The specific importance of the maculations of male legs has necessitated a more precise and morphologically consistent system for designating various portions of the legs than that used by Michener and others. The legs of bees, like those of most insects, may move anteriorly and posteriorly, and may be flexed ventrally and extended laterally. The middle legs, when extended, are nearly perpendicular to the longitudinal axis of the body (presumably the "primitive" condition in the Arthropoda). The fore legs and hind legs, however, are directed respectively forward and rearward to a greater or lesser degree. Owing to the rearward orientation of the hind legs of bees (especially in pinned specimens and in live bees in flight), that which is designated by previous authors as the "inner" surface of the hind legs is not homologous with what they term the "inner" surface of the fore legs.

Therefore, I propose a terminology consistent with the presumed serial homology of the parts of the three pairs of legs rather than with the positions in which they are borne. Although this system may at first seem strange and cumbersome, it is economical in that one can refer, for example, to serially homologous maculations as being on the posterior surfaces of all three pairs of legs. With the system used by other authors one could not refer to such maculations as being on the "inner" surfaces of all three pairs of legs. The disadvantage of the proposed system is that the "dorsal" quadrant of the tarsus may be visible only from below (due to the flexed position of the leg), and the "anterior" surface of the hind leg only from the side.

In the following descriptions, the legs are considered as extended at right angles to a sagittal plane through the body of the bee. The hypothetical leg segment is regarded as cylindrical, its cross-section divided by perpendicular diagonals into dorsal, ventral, anterior and posterior quadrants.

DESCRIPTION. To conserve space, the reader is often referred to the description of another species or sometimes the opposite sex. All interspecific comparisons are between members of the same sex unless otherwise specified.

Because sexual dimorphism is so pronounced in *Agapostemon*, characters used to differentiate males (or females) of two closely related species are not always present on members of the opposite sex. In some instances members of only one sex can be differentiated morphologically. In other cases the morphological differences between species are so subtle as to render identification difficult regardless of sex. For these reasons distributions have been used (especially in the keys) wherever morphological differentiation was difficult or impossible. Of course, no species is recognized solely on the basis of its distribution. The reader must be cautious in relying on distributional differentia because the ranges of species are subject to change without notice.

If two species are very similar then only one is described and the other is described as identical but for the differentiating characters. Relative size is presented as proportions and absolute size may be derived from scale drawings. For each character, the drawings are to the same scale to facilitate size comparisons between species.

Synonymies have been kept as brief as possible and no references to synonyms have been made unless they involve nomenclatural changes of specific epithets. An effort was made to locate and examine the primary types of all nominal species and subspecies and, whenever possible, their location has been noted in the synonymy. In quotations of label data on the types of new species, a single slash indicates the break between lines on a label and a double slash the break between labels on a pin.

KEY TO SPECIES OF THE UNITED STATES
AND CANADA

1. Female; 10 flagellomeres; scopa on hind leg 2
 Male; 11 flagellomeres; scopa absent 14
- 2.(1) Metasomal terga bright metallic green to blue, concolorous with
 head and mesosoma 3
 Metasomal terga black to pale amber, not concolorous with
 metallic head and mesosoma 7
- 3.(2) Wings almost hyaline, only slightly darkened on distal margins;
 mandible yellow basally 4
 Wings transparent brown, distal margins conspicuously dark-
 ened; mandible usually amber basally (rarely yellow) *splendens*
- 4.(3) Mesoscutum with numerous fine punctures interspersed with
 fewer distinctly larger and deeper punctures; punctuation often
 so fine as to leave mesoscutum shiny (Figs. 23, 24)
 *texanus* and *angelicus**
 Mesoscutum coarsely punctate or rugose, lacking punctures of
 two distinct sizes and never shiny 5
- 5.(4) Mesoscutum coarsely rugose at least on inner borders of
 parapsidal lines, if not rugose throughout *femoratus*
 Mesoscutum between parapsidal lines coarsely punctate, not
 rugose 6
- 6.(5) Common in eastern half of U.S., becoming rare in the Great
 Plains (Fig. 18) *radiatus*
 Common on Mexican Plateau and in arid southwestern U.S., rare
 along eastern border of Rocky Mountains (Fig. 2) *cockerelli*
- 7.(2) Posterior lobe of pronotum with pale yellow or creamy spot at
 apex (Fig. 134); clypeus with yellow transverse band (Fig. 42)
 *nasutus*
 Posterior lobe of pronotum metallic at apex, never creamy or
 yellow; clypeus with or without yellow transverse band 8
- 8.(7) Clypeus with transverse apical or subapical yellow band;
 metasoma black or pale amber 9
 Clypeus metallic with apical region dark brown to black;
 metasoma always black 10
- 9.(8) Pronotum with single conspicuous sharp carina extending
 postero-ventrally from lateral angle (Fig. 135); metasomal terga
 black with narrow basal bands of white tomentum; scape dark
 brown to black, lacking yellow *leunculus*
 Pronotum without conspicuous sharp carina extending postero-
 ventrally from lateral angle (may have several small carinulae);
 metasomal terga pale amber to black, with white tomentum on
 basal halves; scape sometimes marked with yellow 12
- 10.(8) Genal ridges coarse (2-3 per 0.25 mm) (Fig. 28); mandible
 usually yellow basally *virescens*
 Genal ridges fine (5-6 per 0.25 mm); mandible amber to brown-
 black basally 11

* The females of *A. texanus* and *A. angelicus* cannot be reliably separated on the basis of their morphology; however, females occurring well outside the range of *A. angelicus* males are probably *A. texanus* (see map, Fig. 20).

- 11.(10) Wings transparent brown; white tomentum lacking on anterior part of first metasomal tergum; protuberance above clypeus without large, central, shiny area *coloradinus*
 Wings hyaline, not brown; white tomentum on anterior part of first metasomal tergum 13
- 12.(9) Dorsal area of propodeum moderately to coarsely rugose; scape often marked with yellow; metasomal terga amber to black or black with amber anteriorly on tergum 1 *melliventris*
 Dorsal area of propodeum finely rugose to finely rugulose; scape never with yellow markings; metasomal terga always entirely black *peninsularis*
- 13.(11) Supraclypeal protuberance with smooth shiny central area with scattered punctures; found only in Arizona, New Mexico and on the Mexican Plateau (Fig. 27) *tyleri*
 Supraclypeal protuberance with weakly and transversely rugose central area; occurs around Gulf of California *mexicanus***
- 14.(1) Clypeus conspicuously concave ventrally, more than three times as broad as long (Figs. 86, 87) *nasutus*
 Clypeus normal, little broader than long 15
- 15.(14) First metasomal tergum yellow to very pale amber basally, not brown or black, and hind basitarsus always slender and simple (Fig. 155); hind leg yellow with small brown or black area apically on femur and basally on tibia *melliventris*
 First metasomal tergum brown to black basally (if pale amber, then hind basitarsus swollen and with basal ridge and apical groove); hind leg usually with dark brown to black stripe on tibia 16
- 16.(15) Hind femur without tooth; slender 25
 Hind femur with subapical tooth postero-ventrally; often conspicuously inflated 17
- 17.(16) Wings transparent brown, conspicuously darkened at distal margins; hind basitarsus with crest of basal ridge grooved (Fig. 166) *splendens*
 Wings hyaline or nearly so, not conspicuously darkened at distal margins; hind basitarsus with basal ridge (if present) not grooved 18
- 18.(17) Metasoma with last two visible sterna (5-6) dark brown to brown-black, without yellow maculations; sterna 2-4 with yellow (if present) restricted to basal margins 19
 Metasoma with extensive yellow maculations on last two visible sterna (5-6) as well as on sterna 2-4 21
- 19.(18) Hind femur lacking brown to black stripe on posterior surface (Fig. 158) *virescens*
 Hind femur with large brown to black stripe covering most or all of posterior surface 20
- 20.(19) Brown to black streak less than $\frac{2}{3}$ length of posterior surface of hind tibia (Fig. 160) *coloradinus*
 Brown to black streak extending entire length of posterior surface of hind tibia (Fig. 159) *tyleri*

** Although not currently known to occur in the United States, this species may yet be found in the vicinity of San Diego or Yuma, thus it is included in this key.

21.(18)	Metasomal sternum 4 (antepenultimate visible) with low transverse ridge not quite reaching posterior margin laterally; metasomal tergum 4 usually without conspicuous metallic tints	22
	Metasomal sternum 4 (antepenultimate visible) with low transverse ridge reaching posterior margin laterally; metasomal tergum 4 nearly always with conspicuous metallic tints	24
22.(21)	Hind basitarsus lacking apical groove and basal ridge (Fig. 161)	<i>radiatus</i>
	Hind basitarsus with apical groove and basal ridge	23
23.(22)	Hind basitarsus with inconspicuous basal ridge and slender apical groove (Fig. 162)	<i>cockerelli</i>
	Hind basitarsus with very large, conspicuous, slightly sinuate basal ridge and broad, conspicuous apical groove (Fig. 163)	<i>femoratus</i>
24.(21)	Base of apical stylus of gonostylus slightly inflated (Fig. 181); brown to black stripe on posterior surface of hind tibia but never on anterior surface (Fig. 164)	<i>angelicus</i>
	Base of apical stylus of gonostylus not inflated (Fig. 180); brown to black stripe anteriorly on hind tibia (Fig. 165), or, if lacking, then without black stripe on posterior surface	<i>texanus</i>
25.(16)	Posterior surface of hind tibia largely yellow (Fig. 143)	<i>leunculus</i>
	Posterior surface of hind tibia largely brown or black	26
26.(25)	2-4 large submarginal bristles on each side of metasomal sternum 4	<i>peninsularis</i>
	14-20 large, evenly spaced submarginal bristles on metasomal sternum 4	<i>mexicanus*</i>

KEY TO MESO-AMERICAN** SPECIES

1.	Males; 11 flagellomeres; scopa absent	2
	Females; 10 flagellomeres; scopa on hind legs	15
2.(1)	Antenna normal	3
	Antenna long, filamentous, and with apical flagellomere flattened (Fig. 131)	<i>rhopalocera</i>
3.(2)	Clypeus normal, little longer than broad	4
	Clypeus conspicuously concave ventrally, more than three times as broad as long (Figs. 86, 87)	<i>nasutus</i>
4.(3)	Metasoma banded with yellow and dark brown or black, lacking bands of white tomentum	5
	Metasoma pale amber, with bands of white tomentum	<i>centratus</i>
5.(4)	Sixth metasomal sternum flat or with inconspicuous medial ridge	6
	Sixth metasomal sternum with medial "button" (flattened process resembling human tongue and attached to sternum in much the same way as human tongue is attached to floor of mouth (Fig. 136)	<i>intermedius</i>
6.(5)	Hind femur with conspicuous subapical tooth postero-ventrally	7
	Hind femur lacking tooth	11

* Although not currently known to occur in the United States, this species may yet be found in the vicinity of San Diego or Yuma, thus it is included in this key.

** Mexico, Panama, and intervening countries.

- 7.(6) Wings hyaline or nearly so, not conspicuously darkened at distal margins; hind basitarsus with basal ridge (if present) not grooved 8
 Wings transparent brown, conspicuously darkened at distal margins; hind basitarsus with crest of basal ridge grooved (Fig. 166) *splendens*
- 8.(7) Metasoma with extensive yellow maculations on sterna; hind tibia with brown or black posterior stripe (when present) not extending from base to apex 9
 Metasoma with sterna brown or black, lacking yellow maculations; hind tibia with broad brown or black posterior stripe extending from base to apex *tyleri*
- 9.(8) Metasomal sternum 4 (antepenultimate visible) with low transverse ridge reaching posterior margin laterally; metasomal tergum 4 nearly always with conspicuous metallic tints 10
 Metasomal sternum 4 (antepenultimate visible) with low transverse ridge not quite reaching posterior margin laterally; metasomal tergum 4 without conspicuous metallic tints *cockerelli*
- 10.(9) Base of apical stylus of gonostylus slightly inflated (Fig. 181); brown to black stripe on posterior surface of hind tibia but never on anterior surface (Fig. 164) *angelicus*
 Base of apical stylus of gonostylus not inflated (Fig. 180); brown to black stripe anteriorly on hind tibia (Fig. 165) or, if lacking, then without black stripe on posterior surface *texanus*
- 11.(6) Base of metasomal tergum 1 dark brown or black 12
 Base of metasomal tergum 1 yellow or pale amber *melliventris*
- 12.(11) Hind leg with broad brown or black stripe covering most of posterior surface of tibia and extending from base to apex; similar stripe on femur sometimes broken centrally 13
 Hind leg largely yellow on posterior surface of tibia and femur 14
- 13.(12) Metasomal sternum 4 with 2-4 large submarginal bristles on each side *peninsularis*
 Metasomal sternum 4 with 14-16 large, evenly spaced submarginal bristles *mexicanus*
- 14.(12) Pronotum with very acute lateral angle; mesoscutum with conspicuous flange laterally on anterior margin *atrocaeruleus*
 Pronotum with lateral angle rounded; mesoscutum lacking flange on anterior margin *leunculus*
- 15.(1) Metasomal terga bright metallic green to blue-green 16
 Metasomal terga pale amber to black, not metallic 19
- 16.(15) Mandibles amber with metallic green spot basally; dorsal area of pronotum with very large, widely separated carinae extending from anterior margin to propodeal carina *aenigma**
 Mandibles amber or yellow, lacking metallic spot basally; pronotum rugose dorsally 17
- 17.(16) Wings almost hyaline, only slightly darkened on distal margins; mandibles yellow basally 18
 Wings transparent brown, distal margins conspicuously darkened; mandibles usually amber (sometimes yellow) basally *splendens*

* Although labeled "Costa Rica" the two specimens of *A. aenigma* are closely related to West Indian species and may be mislabeled.

- 18.(17) Mesoscutum coarsely punctate to finely rugose, lacking punctures of two distinct sizes and never shiny *cockerelli*
 Mesoscutum with numerous fine punctures interspersed with fewer distinctly larger and deeper punctures, punctation often so fine as to leave mesoscutum shiny (Figs. 23, 24)
 *texanus* and *angelicus***
- 19.(15) Lateral angle of pronotum acutely pointed; mesoscutum with conspicuous flange laterally on anterior margin 20
 Lateral angle rounded, not acutely pointed; mesoscutum lacking conspicuous flange on anterior margin 21
- 20.(19) Head and mesosoma black (usually with inconspicuous dark blue tints and with yellow band on clypeus); metasoma black with bands of white tomentum *atrocaeruleus*
 Head and mesosoma metallic green or coppery; metasoma pale amber to black, with yellow integumental bands replacing usual bands of white tomentum *intermedius*
- 21.(19) Posterior lobe of pronotum metallic at apex, never creamy or yellow; clypeus with or without yellow transverse band 22
 Posterior lobe of pronotum with creamy or yellow spot at apex; clypeus with yellow transverse band *nasutus*
- 22.(21) Clypeus with transverse, subapical, yellow band; metasoma amber to black 23
 Clypeus black at apical margin, lacking yellow band; metasoma always black 25
- 23.(22) Pronotum without single conspicuous sharp carina extending postero-ventrally from lateral angle (may have several small carinulae); metasomal terga pale amber to black, with white tomentum on basal halves; scape dark brown to black, sometimes marked with yellow 24
 Pronotum with single conspicuous sharp carina extending postero-ventrally from lateral angle; metasomal terga with narrow basal bands of white tomentum; scape dark brown to black, lacking yellow *leunculus*
- 24.(23) Dorsal area of propodeum moderately to coarsely rugose; scape often marked with yellow; metasomal terga amber to black, or black with amber anteriorly on tergum 1 *melliventris*
 Dorsal area of propodeum finely rugose to finely rugulose; scape never with yellow markings; metasomal terga always entirely black *peninsularis*
- 25.(22) Head and mesosoma bright metallic green 26
 Head and mesosoma black with metallic purple tints *erebus*
- 26.(25) Supraclypeal protuberance with smooth shiny central area and with scattered punctures; occurs in New Mexico, Arizona, and on the Mexican Plateau (Fig. 27) *tyleri*
 Supraclypeal protuberance with weakly and transversely rugose central area; occurs around the Gulf of California *mexicanus*

** The females of *A. texanus* and *A. angelicus* cannot be separated reliably on the basis of their morphology; however, females occurring well outside the range of *A. angelicus* males are probably *A. texanus* (see map, Fig. 20).

KEY TO WEST INDIAN SPECIES

1. Males; 11 flagellomeres; scopa absent 2
Females; 10 flagellomeres; scopa on hind leg 16
- 2.(1) Hind femur without tooth 3
Hind femur with tooth on postero-ventral margin 4
- 3.(2) Lower portion of clypeus abruptly flattened, glabrous and impunctate (Figs. 109-110); metasomal terga yellow with black bands; from Hispaniola, Cuba and Jamaica *kohliellus*
Lower portion of clypeus normal, not abruptly flattened, glabrous (Figs. 121-122) or impunctate; metasomal terga honey-colored; from Haiti *centratus*
- 4.(2) Metasomal terga black or pale amber, never with metallic tints; clypeal region elongate 5
Metasomal terga with yellow and brown to black bands, often with metallic tints; clypeal region normal 9
- 5.(4) Head and mesosoma bright metallic green to blue 6
Head and mesosoma shiny brown-black, not metallic; from Cuba *obscuratus*
- 6.(5) Metasomal terga dark brown to black, pale bands of tomentum conspicuous 7
Metasomal terga pale amber with brown bands, pale bands of tomentum inconspicuous or absent 8
- 7.(6) Sculpturing of mesosoma slightly finer than that of *viridulus*, contiguous punctures giving the mesoscutum a dark blue appearance when viewed from above; from Hispaniola *hispaniolicus*
Sculpturing of mesosoma slightly coarser than that of *hispaniolicus*, subcontiguous punctures giving the mesoscutum slightly shiny green to blue reflections; from Cuba *viridulus*
- 8.(6) Basal ridge of hind basitarsus very broadly and deeply grooved (Fig. 147); mesoscutellum extremely shiny, only weakly sculptured; from Jamaica *swainsonae*
Basal ridge of basitarsus very narrow and without broad, deep groove (Fig. 149); mesoscutellum weakly shiny with contiguous punctures; from Cuba *cubensis*
- 9.(4) Eye normal brown; pterostigma translucent amber to dark brown 10
Eye and (or) underside of pterostigma (except for dark margins) pale cream colored to opaque yellow 14
- 10.(9) Metasomal tergum 3 weakly to strongly metallic green to blue medially 11
Metasomal tergum 3 without metallic green to blue medially 13
- 11.(10) Metasomal tergum 1 with metallic green to blue tints posterolaterally 12
Metasomal tergum 1 without metallic green to blue tints posterolaterally; from Hispaniola *insularis*
- 12.(11) Hind femur 60% as wide as long (Fig. 146); from Jamaica .. *jamaicensis*
Hind femur less than 55% as wide as long (Fig. 144); from Cuba, Hispaniola, New Providence I. and probably from Andros I. and Cat I. *poeyi*

- 13.(10) Metasomal terga 4 and 5 with conspicuous metallic green tints medially; from San Salvador I. (=Watling I.) *columbi*
 Metasomal terga 4 and 5 without conspicuous metallic green tints medially (may have faint metallic tints laterally); from Puerto Rico (including Mona I. and Vieques I.) and New Providence I. *viequesensis*
- 14.(9) Pedicel, unlike scape or flagellum, pale amber to yellow below 15
 Pedicel, unlike scape or flagellum, dark brown below; from Crooked I. *cyaneus*
- 15.(14) From Long I. *sapphirinus*
 From Cat I., Rum Cay, Conception I., New Providence I. and Mariguana (=Mayaguana?) I. *ochromops*
- 16.(1) Metasomal terga black to pale amber, not metallic 17
 Metasomal terga largely metallic green to blue to purple 22
- 17.(16) Lower portion of clypeus brown or black, metasomal terga pale amber to black, lacking yellow bands 18
 Lower portion of clypeus with broad yellow band; metasomal terga with yellow bands; from Hispaniola, Cuba and Jamaica .. *kohliellus*
- 18.(17) Metasomal terga uniformly brown-black with narrow, white bands of tomentum 19
 Metasomal terga 1 and 2 honey-colored becoming brown-black on posterior terga; from Hispaniola *alayo*
- 19.(18) Head and mesosoma metallic green to blue 20
 Head and mesosoma shiny brown-black, not metallic; from Cuba *obscuratus*
- 20.(19) More than 50% of interocular area above antennal sockets and below median ocellus rugose to rugulose 21
 More than 50% of interocular area above antennal sockets and below median ocellus with fine, deep, contiguous punctures; from Hispaniola *hispaniolicus*
- 21.(20) Mandible with metallic green tints basally, about as dark ferruginous-brown basally as apically; from Cuba *viridulus*
 Mandible without metallic green tints basally, much darker apically than basally; from Jamaica *swainsonae*
- 22.(16) Metallic coloration dark blue or dark purple 23
 Metallic coloration green 24
- 23.(22) Gena with fewer than 10 extremely coarse carinae; tegula and legs with some pale amber areas; from Long I. *sapphirinus*
 Gena with many more than 10 fine carinae; tegula and legs dark brown; from Crooked I. *cyaneus*
- 24.(22) Eye normal brown; pterostigma translucent amber to dark brown 25
 Eye or underside of pterostigma (usually both) pale cream-colored to opaque yellow; from Cat I., Rum Cay, Conception I., New Providence I. and Mariguana (=Mayaguana?) I. *ochromops*
- 25.(24) Mandible with metallic green spot basally 26
 Mandible lacking metallic green spot basally; from Puerto Rico (including Mona I. and Vieques I.) and New Providence I. .. *viequesensis*
- 26.(25) Metasomal sterna 3 and 4 with conspicuous medial metallic green tints 27
 Metasomal sterna 3 and 4 brown, without medial metallic green tints 28

- 27.(26) Mesoscutum rugose laterally along parapsidal line, becoming coarsely rugose anteriorly, punctate centrally and posteriorly; from Cuba, Hispaniola, New Providence I., Cat I. and Andros I. *poeyi*
 Mesoscutum finely punctate, with extreme antero-lateral margin rugulose; from Hispaniola *insularis*
- 28.(26) Scopal hairs on femur and hairs on postero-ventral surface of hind tibia golden; from San Salvador I. (=Watling I.) *columbi*
 Scopal hairs on femur and hairs on postero-ventral surface of tibia white; from Costa Rica *aenigma**

KEY TO SOUTH AMERICAN SPECIES

1. Female; 10 flagellomeres; scopa on hind leg 2
 Male; 11 flagellomeres; scopa absent 10
- 2.(1) Mesoscutum rounded on anterior margin; lateral angle of pronotum inconspicuous and not projecting antero-laterally 3
 Mesoscutum with acute upturned flange on anterior margin; lateral angle of pronotum conspicuous and projecting antero-laterally 5
- 3.(2) Pronotum with creamy or yellow spot at apex of posterior lobe and without carina extending postero-ventrally from lateral angle (Fig. 134) *nasutus*
 Pronotum without creamy or yellow spot at apex of posterior lobe and with conspicuous sharp carina extending postero-ventrally from lateral angle (Fig. 135) 4
- 4.(3) Metasoma black; lateral angle of pronotum rounded; 3 spatulate teeth on posterior hind tibial spur *leunculus*
 Metasoma amber; lateral angle of pronotum angular; 5 (rarely 4?) spatulate teeth on posterior hind tibial spur *ascius*
- 5.(2) Metasomal terga 2 and 3 amber or black with yellow basally (best seen in posterior view) 6
 Metasomal terga 2 and 3 amber or black but lacking yellow *semimelleus* or *chapadensis**
- 6.(5) Head and mesosoma dull coppery, metallic greenish-black or bluish-black; mesoscutal pubescence dense and woolly; restricted to western South America 7
 Head and mesosoma usually bright metallic green (may be coppery in Central America); mesoscutal pubescence not especially dense and finely branched; Central and South America *intermedius*
- 7.(6) Propodeum metallic blue-black or green-black dorsally; clypeus without yellow maculations *heterurus*
 Propodeum metallic coppery dorsally; clypeus usually with yellow maculations 8

* *Agapostemon aenigma* is included in this key because its similarity to West Indian species casts doubt on the correctness of its "Costa Rica" label. A specimen with identical label data belongs to the Haitian species *A. centratus*.

* The females of these species cannot be distinguished reliably (cf. *A. semimelleus*, VARIATION).